

# THE TAXONOMIC SIGNIFICANCE OF EVOLUTIONARY PARALLELISM<sup>1</sup>

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The recognition by Darwin that the natural system of classification is in essence an evolutionary system is a major landmark in taxonomic history. Let me read you a passage from Chapter 14 of *Origin of Species*: "... The Natural System is founded on descent with modification . . . the characters which naturalists consider as showing true affinity between any two or more species, are those which have been inherited from a common parent, all true classification being genealogical . . . community of descent is the hidden bond which naturalists have unconsciously been seeking. . . ." A corollary of this principle is that a natural taxonomic group is per se monophyletic, and that polyphyletic groups are in contrast artificial and should be rejected.

Those concepts have become so firmly entrenched in taxonomic thinking as to approach the status of dogma. However, as we learn more about phylogeny, a strict and literal application of the monophyletic requirement in taxonomy has gotten us into more and more trouble. More and more groups that have been considered to be natural are turning out not to be strictly monophyletic. They may be natural in the sense that all the included subgroups are evolutionarily closely related and have many features in common, but they are not monophyletic in the sense of being descended from an original species of the group which has all the essential characters of the group.

The mammals are an outstanding example, with a well documented fossil record, of a natural taxonomic group which is clearly not monophyletic in the strictest sense. We shall return to this fact in a few minutes.

The angiosperms, a large and highly natural taxonomic group of plants, cannot yet be traced back to a common ancestor by means of fossils, but on the basis of comparative morphology of the living members it is very probable that the eventual ancestor of all angiosperms was not itself an angiosperm, but rather a gymnosperm. The characteristic xylem vessels of angiosperms have evidently originated several times among the primitive members of the group. Stages in the development of the closed carpel, usually regarded as an essential feature of angiosperms, can be observed among the living members of the primitive order Ranales. Within the Ranales one can also see all stages

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in the evolution of the typical angiosperm stamen from the ancestral microsporophyll with embedded sporangia. Furthermore, it seems clear, again on the comparative morphology of living species, that the development of the closed carpel and the typical angiospermous stamen with filament and anther took place in several related evolutionary lines within the Ranales, in parallel fashion, rather than being strictly monophyletic. Differentiation of the perianth into calyx and corolla has likewise taken place independently in various families, as has also the origin of petals from staminodes.

Double fertilization and the extreme reduction of the female gametophyte are about all we have left as characters unique to the angiosperms and uniformly expressed in primitive as well as advanced members. Even these characters are suppressed in certain apomictic forms, although the suppression is doubtless secondary. There is no reason to believe that these embryological characters, on whose evolutionary history we have no very good evidence, are any more nearly monophyletic than the characters of vessels, perianth, stamens, and carpels. On the contrary, whenever we do get reasonable evidence on the phylogeny of characters which mark major taxonomic groups, it generally turns out that these develop through parallel evolution in the various closely related but separate lines which collectively make up the ancestral stock of the group.

This same problem with the monophyletic requirement, often in an even more severe form, permeates our whole system of classification. The tribes of the Compositae do not in general represent strictly monophyletic groups; rather they are constellations of genera which show certain evolutionary trends in common and are to some extent linked by transitional species. If my concepts of relationships within the family are correct, the hypothetical ancestor of all the genera of the Astereae would be placed not in the Astereae, but in the Heliantheae; similar statements could be made about most of the other tribes. The common ancestor to all species of the genus *Achaetogeron* would surely be placed in *Erigeron*, if we had it, rather than in *Achaetogeron*. Although I would not yet want to be firmly committed to this next statement, I suspect that the common ancestor to all species of *Baccharis* would be an *Archibaccharis*, the common ancestor to all species of *Archibaccharis* would be a *Conyza*, and the common ancestor to all species of *Conyza* would be an *Erigeron*. The most primitive existing species of *Erigeron*, in turn would on morphological grounds be just as well referred to *Aster*, and in fact it was first described as *Aster peregrinus* Pursh. It is now referred to *Erigeron* mainly because of its obvious relationship to species which are necessarily included in *Erigeron*.

The difficulties attendant on a strict application of the monophyletic concept in classification have led a few taxonomists in recent years to exclude the concept entirely from taxonomic theory and practice, to

attempt to divorce phylogeny from taxonomy. I recognize the problems these people have felt, and I sympathize with their struggles, but I disagree with the proposed solution. It is the evolutionary concept which has given meaning to the whole idea of a natural system, just as Darwin said it would. An attempt should therefore be made to resolve the conflict, rather than to dissolve what has been a most fruitful union.

I believe the conflict is resolvable, and the terms of the resolution have already been laid down, now 17 years ago, by George Gaylord Simpson. In 1945 he pointed out that the monophyletic requirement must be interpreted broadly in order to be useful taxonomically (see "The principles of classification and a classification of mammals," American Museum of Natural History Bulletin, vol. 86). Again, let me quote: "The condition that classification must be consistent with phylogeny has as its most important corollary the requirement that all the animals within a given group, whatever its rank, must have had a common origin. . . . The principle that the units of classification must have a unified origin, or be monophyletic, easily leads to absurdity if not reasonably interpreted. Its complete *reductio ad absurdum* is the suggestion that each group must have originated from a single pair of animals, a requirement that has perhaps never been fulfilled in the history of life and that certainly cannot be demonstrated in any case. The rule that a group, to be considered monophyletic, must be derived from a single species of a preceding group is more reasonable and can sometimes be met in practice, but it also requires qualification. It is not at all clear that practical classification could consistently meet this requirement if phylogenetic knowledge were complete. In fact, knowledge is so far from complete that adherence to such a rule would lay classification open, to an unnecessary and undesirable degree, to the caprices of shifting theory and individual opinion. It is not useful to set up a classification in which groups with different names cannot be distinguished morphologically, but this does happen if theoretical monophyly is too strictly demanded. . . . Given a group that is composed of related animals and defined by morphological and related data, the most practical and, at least for the present, the most desirable additional requirement seems to be not that it should be derived from one immediately antecedent genus or species, but, with intentional vagueness, that its immediate ancestry should be included within a group of lower rank than itself. For instance, it is not probable on the basis of present knowledge that all the animals here included in the Mammalia arose from the Reptilia as a single species, genus, or even family, but it is not suggested on this account that some of them should be returned to the Reptilia or that another class should be created for them. They certainly arose from a unified group of reptiles of much smaller scope than a class, perhaps a family or perhaps a superfamily, and for practical purposes this is an adequate fulfillment of the requirement of monophyly."

To recapitulate, if a taxonomic group of a particular rank is derived wholly from another group of lower rank, that is a sufficient degree of monophyly for taxonomic purposes. Dr. Simpson has very recently (1961, in his book *Principles of Animal Taxonomy*) modified this concept to read "of the same or lower rank," and here I feel he may have gone a bit too far. His point, however, is well taken. Monophyly and polyphyly are not such utterly distinct things as the terms would suggest. There is a continuous gradation from the strictest monophyly to the most utter polyphyly in proposed taxonomic groups. In order to be natural and acceptable, a taxonomic group must fall somewhere toward the monophyletic end of this scale, rather than toward the polyphyletic end.

It now appears that a workable taxonomic system cannot provide a perfect reflection of evolution, no matter how abundant the evidence on which it is based. Furthermore, conclusions must usually be based on more or less inadequate evidence; none of us has witnessed the events of geologic time. But the phylogenetic concept still provides the underlying rationale for the natural system. Taxonomy can provide only a somewhat muddy reflection of evolution, but a reflection all the same.

Once we admit the broad interpretation of the monophyletic requirement, as I believe we must do in order to have a workable system, then we are committed to the position that similarities due to evolutionary parallelism, as well as those due strictly to inheritance from a common ancestor, provide some indication of relationship and should be considered in the formulation of the taxonomic system. Just how much weight should be given to parallelism is another question, to which we will return later.

As long ago as 1912 Wernham pointed out that "critical tendencies are no less important than critical characters" (see the final paper in his series on floral evolution in the *New Phytologist*, vol. 11). He further pointed out that "the general relation between the significant features of the ancestry and those of the descendants is, that in the former the characters in question are not constant throughout the group, nor may they be completely evolved. In other words, we are dealing with *tendencies* to characters, and not with the critical characters themselves, in the case of the ancestry. In the progeny, on the other hand, the characters are constant and completely evolved; and the line which unites ancestor and descendants represents the transition between the tendencies and their realization." He goes on to provide several examples. Probably most of us here can provide equally good examples from our own experience.

The proposition that similarities due to common descent, to inheritance from a common ancestor, indicate relationship is of course self-evident. We have pointed out that taxonomists have been forced, on a pragmatic basis, to accept also the proposition that similarities due to

parallelism also provide some evidence of relationship. Let us now proceed to an inquiry into why this should be so, or how it can be so.

A concise expression of the most generally accepted present concept of the mechanism of evolution would be something like this: Random mutation and natural selection, modified by the influence of happenstance survival in small populations. I submit that random is the wrong word here, and that it has had an unfortunate effect on our thinking. To me, and I think to many other people, random implies that any one thing is as likely as any other thing. Thus in a table of random numbers, any one number in the series is as likely in any particular slot as any other number. Mutations are at random only in the sense that there is a large element of chance, and that we cannot control or predict them individually; they are certainly not at random in the sense of one mutation being as likely as any other. It is abundantly clear that the different mutations which can occur in a particular gene do not occur with equal frequency, nor is the mutation rate from one allele to another the same in opposite directions. There are even genes which influence the rate and direction of mutation in other genes. All this is well known to geneticists. As long ago as 1940 Dobzhansky stated that mutability, like other characteristics, is under partial genetic control.

The proposed statement of evolutionary mechanism would thus be more accurate if the word differential were substituted for random: Differential mutation and natural selection, modified by the influence of happenstance selection in small populations. With this phraseology, it is more obvious that not all evolutionary channels are open to any one group, and that different groups will have different evolutionary potentialities. At the grosser levels this is of course immediately obvious anyway. An oak doesn't have much chance of evolving into a carnivore, nor is a dog likely to develop photosynthesis. But it is also true at other, less obvious levels. The Solanaceae and Scrophulariaceae are so closely related that it is difficult to draw a precise line between them, but as Dr. H. A. Gleason has pointed out to me in conversation, they differ in their evolutionary potentialities for the production of certain types of chemicals. The Solanaceae very often produce alkaloids; in Wernham's terminology, they might be said to have a critical tendency toward the production of alkaloids. The Scrophulariaceae only very rarely produce alkaloids, although they do sometimes produce glycosides.

The occurrence of diffuse centromeres in *Luzula*, *Juncus*, and certain genera of the Cyperaceae is one more evidence of the generally recognized affinity between the Juncaceae and Cyperaceae. It is significant to our discussion that although the Cyperaceae are on both floral and vegetative characters the more advanced of the two families, only some of the cyperaceous genera have diffuse centromeres, whereas others have the more standard point centromeres. It seems very probable, then,

that the occurrence of diffuse centromeres in these two families represents a case of parallelism rather than of inheritance from a common ancestor. I should add, of course, that no one character by itself provides proof positive of relationship; diffuse centromeres also occur in *Spirogyra*. Nevertheless, the occurrence of this rare character in the Juncaceae and Cyperaceae suggests that these two families have in common an unusually high potentiality to evolve in this direction. Some of the foregoing information on the occurrence of diffuse centromeres was provided for me by John Ebinger.

*Clarkia* and *Oenothera* provide another example at a lower taxonomic level. Here I get my information, as you might guess, from Harlan Lewis. *Clarkia* characteristically occurs in dry country, bordering deserts, but not actually in them. Individual colonies at the drier margins of the range lead a precarious existence, and are subject to being wiped out in bad years. The plants are annual, and the seeds germinate as soon as the moisture and temperature conditions are right. If the moisture supply then fails before the seeds are mature, no seeds are left over to begin again the following year. It appears that the one thing *Clarkia* lacks to be a potentially successful desert annual is a variable period of dormancy, so that some seeds would last over until the second or third year, regardless of how favorable conditions may be in the interim. In the many thousands, perhaps millions of years that *Clarkia* has occupied a habitat in which such a change would have a strong survival value, it appears to have been unable to evolve such a feature. Presumably the proper mutations just have not occurred. The closely related genus *Oenothera*, on the other hand, occurring in similar habitats, has in several lines given rise to desert species with a variable period of seed dormancy. There is nothing in the obvious characteristics of the plants to suggest that the evolution of desert species should be easier for the one genus than the other; the difference instead appears to lie in the mutative potentialities.

Now let us return to theoretical considerations. The existence of the same character in two different groups may be due either to their having inherited the character directly from a common ancestor, or to their having developed the character independently by parallel evolution. We are concerned here only with the second situation, not the first. If the character was independently developed in the two groups, it is still true, at the very least, that their respective ancestors had similar evolutionary potentialities with regard to that character, and thus were genetically similar—not necessarily identical—in this particular respect. Thus, evolutionary parallelism with regard to a particular character is one straw in the wind, indicating a degree of similarity and possible relationship among the ancestors. Now if we add another character in which these same two groups resemble each other, by parallel evolution, we have two straws in the wind, and so on. Thus, the more char-

acters the two groups have in common, the greater must have been the genetic similarity of the ancestors of these groups—even though they did not have the characters under consideration, and the possession of these characters by the modern descendants is due to parallel evolution rather than direct inheritance from a common ancestor. Furthermore, the less common a particular character is in other groups, the more significant its independent development in two lines becomes, as an indicator of relationship.

Therefore, we come to the general principle that evolutionary parallelism tends to indicate relationship, and that it should be given due weight, along with other factors, in arriving at taxonomic conclusions. This is true regardless of whether one believes that all evolutionary trends must be explained in terms of survival value, or whether one believes, as I do, that some evolutionary trends are essentially orthogenetic and not directly related to survival value. Now, for purposes of argument, let us assume that I am correct in believing that there is every gradation from evolutionary trends which are essentially Darwinian to those which are essentially orthogenetic. Then, the greater the selective control, the less the taxonomic significance of the parallelism, and vice versa. If the control is essentially selective, then all the similarity that is required between the ancestors is the *ability* to produce the necessary mutations; selection does the rest. If the control is essentially orthogenetic, the ancestors must be sufficiently similar so that both of them produce these mutations in considerably greater frequency than other mutations, so that the mutation pressure, operating along with the other causes of speciation, can cause parallel evolutionary developments.

On theoretical grounds, therefore, characters which are not closely correlated with survival value and ecologic niches are likely to be more important taxonomically, in many instances, than characters which are directly influenced by selection. This is especially true in the angiosperms, in which the evolutionary barriers between different ecological niches are frequently minimal, and one family may fill highly diverse niches.

On purely pragmatic grounds, plant taxonomists over the last two centuries have come to this same operating principle. The characters used to distinguish the families and orders of angiosperms are in large measure things which are difficult to relate to Darwinian evolution. Such things as hypogyny, perigyny, and epigyny; polypetaly, sympetaly, and apetaly; apocarpy and syncarpy; placentation; numbers of floral parts of each kind, and the like. I hasten to point out, however, that the situation in the vertebrates is different. There the whole structure of the organism is intimately correlated with the way it makes its living: what kind of food it eats, how it captures that food, and how it keeps from being used as food by something else. Here the evolutionary bar-

riers between different ecologic niches are formidable, and within each general niche the selective pressures operating on different but related taxa tend to be similar, and different from the selective pressures operating on taxa occupying different general niches. I have pointed out elsewhere that this difference in mode of evolution is responsible for the great difficulty of recognizing and defining the families and orders of angiosperms, as contrasted with the relative ease with which such groups are recognized in the vertebrates—but that is another story.

It is interesting to note that Wernham, with no knowledge of genes and not very much knowledge of heredity, also came to the conclusion that nonadaptive characters are more likely to be important than adaptive ones. He spoke of "biological" characters, which are directly related to some vital function or advance, and "fortuitous" characters, which have no relation to the environment nor to any biological function. He concluded that "A group of plants may share a number of biological characters in common without being therefore nearly related," but, on the contrary "The occurrence of several common fortuitous characters in a series of plant-forms is valid evidence of their mutual affinity; and the greater the number of common characters, the closer the affinity." To this I would add simply that this evidence is significant even if the similarities are due to parallel evolution instead of direct inheritance from a common ancestor.